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CONTENTS OF VOL. X.

No. 1. December, 1905

Page

Adele M. Fielde: *The Progressive Odor of Ants* 1

E. H. Harper: *Reactions to Light and Mechanical Stimuli in the Earthworm Perichæta Bermudensis (Beddard)* 17

Lulu F. Allabach: *Some Points Regarding the Behavior of Metridium* 35

No. 2. January, 1906

R. R. Bensley: *An Examination of the Methods for the Microscopical Detection of Phosphorus Compounds other than Phosphates in the Tissues of Animals and Plants* 49

J. F. McClendon: *On the Locomotion of a Sea Anemone (Metridium marginatum)* 66

H. H. Newman: *The Significance of Scute and Plate "Abnormalities" in Chelonia* 68

No. 3. February, 1906

H. H. Newman: *The Significance of Scute and Plate "Abnormalities" in Chelonia* 99

T. B. Robertson: *Note on the Influence of Surface-Evaporation upon the Distribution of Infusoria* 115

Vernon L. Kellogg: *Histogensis in Insect Development, and Cell Specificity* 120

E. A. Andrews: *Ontogony of the Annulus Ventralis* 122

No. 4. March, 1906

O. C. Glaser: *Correlation in the Development of Fasciolaria* 139

Charles S. Rogers: *A Chameleon-like Change in Diemyctylus* 165

A. C. Eycleshymer: *The Growth and Regeneration of the Gills in the Young Necturus* 171

W. L. Tower: *Observations on the Changes in the Hypodermis and Cuticula of Coleoptera During Ecdysis* 176

158450

No. 5. April, 1906

PAGE

ESTHER F. BYRNES: *Two Transitional Stages in the Development of Cyclops signatus, var. coronatus* 193

T. H. MORGAN: *The Male and Female Eggs of Phylloxerans of the Hickories* 201

CHAS. W. HARGITT: *The Organization and Early Development of the Egg of Clava leptostyla Ag* 207

PHILIP B. HADLEY: *Regarding the Rate of Growth of the American Lobster* 233

T. B. ROBERTSON: *Note on the Influence of Temperature upon the Rate of the Heart-beat in a Crustacean (Ceriodaphnia)* 242

L. B. SEELY: *Two Distomes* 249

No. 6. May, 1906

INEZ L. WHIPPLE: *The Ypsiloid Apparatus of Urodeles* 255

FRANCIS B. SUMNER: *The Osmotic Relations Between Fishes and their Surrounding Medium (Preliminary Note)* 298

Vol. X. *December, 1905.* *No. 1*

BIOLOGICAL BULLETIN

THE PROGRESSIVE ODOR OF ANTS.

ADELE M. FIELDE.

I. Statement of Hypotheses Based on Recent and Former Experiments.

1. *The Specific Odor.* — The mother-ant transmits to her offspring the distinctive odor which is identical for ants of all ages and of both sexes within the species. This odor is appreciated among ants by organs near the proximal end of the funicle.[1]

2. *Progressive Odor.* — Female ants, including queens and workers, have, besides their specific odor, an odor which may be termed progressive. Queens of different lineage have different progressive odors. In a queen this odor is either unchanging or changes very slowly, and it is similar to that of her newly-hatched female offspring.

a. As worker-ants advance in age their progressive odor intensifies or changes to such a degree that they may be said to attain a new odor every two or three months. This progressive odor is appreciated among ants by organs in the penultimate joint of the funicle.[2]

b. Male ants have no progressive odor unless it be superficially incurred through association with workers; but the male carries latent in his spermatozoa the progressive odor of his mother. In other words the progressive odor is always recessive in the male ant.

c. The progressive odor of each new generation of females is

[1] "Artificial Mixed Nests of Ants," A. M. Fielde, Biological Bulletin, Vol. V., No. 6, November, 1903, p. 320.

[2] "Farther Study of an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences*, November, 1901, p. 531.

determined by the odor of the mother latent in her egg, and the odor of the father's mother latent in the spermatozoön. The progressive odor therefore changes in each generation of females.

d. The progressive odor manifest in female ants is the cause of the separation of ants of the same species into hostile colonies, and is of great advantage to the ants in their individual and their communal life.

3. *The Incurred Odor.* — An ant may incur from its associates an odor which is not inherent in itself, and which may be removed by washing. It may be transferred from ant to ant through air or through water. It arises from the substances that give the specific odor and the progressive odor and that create the nest-aura.

II. Recent Experiments with the Progeny of a Single Queen, Componotus Pennsylvanicus.

In 1901 I found that the odor of working-ants of *Stenamma fulvum piceum* changes with their age,[1] forty days being the minimum of time in which there occurs a change so great as to effect the behavior of ants of the same colony toward one another at their first meeting.

In 1902 my further experiments indicated that a cause[2] for the hostility of one colony toward another of the same species and variety is a difference in odor coincident with difference in the age of the colonies.

In 1904 my observations on several species of ants,[3] representing three subfamilies, gave further evidence of their change of odor with advance of age, and indicated that the odor of the queen is unchanging, or that her odor changes much more slowly than does that of the workers.

I have now had under observation for more than two years a colony of *Camponotus pennsylvanicus*, in which the assertion of a

[1] "A Study of an Ant," *Proceedings of the Academy of Natural Sciences of Philadelphia*, July, 1901, p. 449.

[2] "Notes on an Ant," *Proceedings of the Academy of Natural Sciences of Philadelphia*, September, 1902, p. 609; "Cause of Feud Between Ants of the Same Species," Biological Bulletin, Vol. V., No. 6, November, 1903, p. 328.

[3] "Power of Recognition Among Ants," Biological Bulletin, Vol. VII., No. 5, October, 1904, p. 244.

progressive odor in the workers is definite and indisputable, the five successive broods included in the experiment being the issue of one queen.

The N Queen. — This queen was captured on Nonamesset Island, July 28, 1903. She was then deälated and was probably the mother of the hundred workers seen in her wild nest, and also of the ants that afterwards hatched from the many cocoons brought with her to the laboratory. She remained under my care and, unless another is indicated, she is the queen referred to in the herein recorded experiments.

The N1 Group of Workers. — Some of the captured workers were transferred to Dr. Irving A. Field, and they remained segregated in his care, usually at Harvard University, until the time of the experiment in which they appear. As no other than male offspring had appeared in this group during the two years of its separation from the queen mother, the workers composing it in August, 1905, were certainly acquainted with the queen previous to her capture in July, 1903. Of the age of these workers of course nothing more was known than that it exceeded two years.

On August 6, 1905, I introduced into this nest,[1] where there were six major and five minor workers and about thirty larvæ from their own eggs, the queen-mother from whom these eleven workers had been separated for two years. The queen showed instant hostility, seized a major worker by one of its mandibles, braced herself on the sponge and held her prisoner there during the ensuing seven hours. All the other workers, sometimes six at a time, examined the queen meanwhile. They patted her with their antennæ, nabbed her gently, and licked her back and legs. Two of them, touching her body with their antennæ, appeared to dance for joy, shuffling their feet with great rapidity during several consecutive minutes. The queen then began to drag the worker that she had seized, and upon my releasing the latter, took a position near the larvæ-pile, as if to claim her incipient grandsons as her exclusive property, opening her mandibles at every worker who approached. Then followed a most curious and pro-

[1] All the artificial nests referred to in this paper were of the Fielde pattern. See "Portable Ant-Nests," BIOLOGICAL BULLETIN, Vol. VII., No. 4, September, 1904.

longed effort on the part of the workers to placate the queen-mother. They surrounded her at all times, offering her regurgitated food. Whichever way she turned, there stood a humble servant with a proffered mouthful of pabulum. As many as seven workers simultaneously offered nourishment to her. Every worker of the eleven seemed bent upon wooing and winning her, and she was not for a moment left without attention. These efforts were unceasingly continued, and were meeting with a fair degree of success, when I removed the queen on the following morning.

This experiment showed that the workers all recognized the odor of their queen after two years of separation from it, and that the segregated workers had during the same interval acquired an odor unfamiliar to the queen, who had meanwhile met none of her daughters who were over fifteen months old. It also showed that major workers, having in this species nearly the same form and sometimes nearly the same bulk as has the queen, are like minor workers in having a progressive odor.

On August 7 I introduced into this N1 group a marked major and a marked minor worker, daughters of the N queen, but many months younger than any of the ants in this group. The visitors were received with signs of curiosity, but with perfect amiability, though no younger sisters had been encountered within two years by these N1 ants. The odor of the younger sisters was perfectly recognized by the eleven residents, and I removed the former.

I then introduced a young winged queen of the same species, *Camponotus pennsylvanicus*, but of an alien colony. The resident ants attacked her instantly and with exceeding virulence. In an instant she lost an antenna, one worker was pulling out her remaining antenna, and three others were dragging her by her legs. The scrimmage was fierce, and before I removed the intruder four of the residents had received injuries that resulted in their deaths. The residents had given to the alien queen a reception strongly contrasted with that accorded to their own queen-mother; while the havoc wrought by the alien queen indicated that, if unable to escape from the nest, she might have destroyed all the workers and have remained a fostering mother to their larvæ.

The N2 group. — During the first week in August, 1903, the queen deposited about a hundred eggs, and from these were reared five minor workers, denoted here as the N2 ants. These workers hatched between April 24 and May 10, 1904, and were therefore some fifteen months old at the time of the experiment here recorded. These workers had never met other ants than those of their own segregated group, and were therefore unacquainted with the odor of ants in any wise unlike themselves. They had never lived with the queen, had laid no eggs, and had the care of no young. On July 16, 1905, I put these ants into a new and very small nest where I had isolated the queen-mother without young. The five workers were wholly at ease with the queen, and hastened to evince their devotion in ant fashion; but the queen opened her jaws whenever they approached her, and was somewhat querulous in her behavior during the ensuing two days. The queen had lived during the previous five months with daughters, all minor ants, less than five months old, and her behavior indicated a difference in the odor of her younger and her older daughters. Her memory was manifestly less tenacious than that of the workers, who, on their part recognized in their queen the odor that had been their own in their infancy, fourteen months earlier.

The N3 group. — This group consisted of two major workers hatched in July, 1904, and four of their younger sisters, minor workers, over five months and less than a year old, all the issue of the N queen. The two majors were acquainted with sisters older than themselves, while the minors knew no sister older than these two majors. The members of this group had all lived with the queen, and had been separated from her and living in segregation since February 14, 1905. They had deposited no eggs, and they had the care of a few introduced larvæ. On July 18, 1905, I introduced into this group a sister nine months older than the oldest in the group. The majors, who had had acquaintance with sisters much older than themselves, did not attack the newcomer at all, while every one of the minors, never having met a sister so old as was the visitor, attacked, dragged and finally killed her.

It appeared that the behavior of the two major workers was

dictated by memory, while that of the four minor workers was an effect of hostility created by the presentation of an unfamiliar odor. The major workers were either wanting in compassion, or else they lacked means of communicating with their younger sisters, for although they were each double the size of any minor ant in the group, they did not interfere in behalf of the victim.

The N4 Group. — The queen was transferred without eggs or young to a new nest on July 14, 1904. She laid no eggs thereafter until December, 1904, and from the eggs then deposited the five minor workers constituting the N4 group were hatched between February 19 and March 23, 1905. These workers were therefore four or five months old at the time of the experiment. On July 16, 1905, I removed the queen from the nest, leaving the five workers in charge of twenty larvæ, the issue of the queen's December eggs. Into this group of five minors, who had never met older sisters, I introduced one of the majors from group N3, now just a year old, and twice or thrice the bulk of any of the five residents. The introduced ant was instantly and violently attacked by three residents. This attack indicates that the major, like the minor ants, like in shape and size as they are to the queen, change their odor with advance in age, as do minor workers.

Having removed this visitor, I introduced a marked large minor worker, fourteen months older than the residents, a sister of theirs, hatched from eggs deposited by the queen in August, 1903. This visitor was likewise violently attacked, every one of the five residents manifesting hostility to her, and the next day I found her mangled body on their rubbish pile.

The N5 Group. — This group consisted of two minor workers, the issue of the queen's December eggs, sequestered in their cocoons and hatched on September 8, 1905. They were at once placed in segregation in a new nest, with a few larvæ and cocoons from their mother's eggs. Ten days later these ants drove away from their pile of young any member of the N4 group of sisters six months older than themselves.

In these experiments it appears that it is the age of the workers, not the age of the queen at the time when she deposits the eggs from which the workers issue, that determines at any date

their progressive odor. All the ants engaged in this last mentioned experiment were certainly the issue of the eggs laid by the queen early in December, 1904. That there is similar progress in odor among ants of the same age and species is indicated by an immediate and amicable association of ants that are reunited after a period of separation so long as two years.[1]

Whether two mutually hostile groups could be created from among the worker-progeny of a single queen would depend on power of memory in the older workers. By segregating from the pupa-stage the broods of different summers, it would be found that the younger sisters would always be hostile to the older sisters, because the older sisters would present an unfamiliar odor to the younger. The hostility of the older sisters toward the younger would be nullified by their memory of the odors by which they had themselves been characterized at earlier periods in their own lives. If the younger sisters bore an odor which the older sisters, through the lapse of many years, should have forgotten, then the hostility would become mutual. It is certain that worker-ants can remember for years an odor with which they have once become familiar, and it is probable that they remember such odors as long as they live.

When ants of different groups meet amicably, either the members of these groups have the same odor, or else they have at some time in their lives been familiar with ants bearing the presented odor. If one group recognizes a familiar odor, while the other group discerns a strange odor, then those finding themselves among strangers will try to escape, or will make attack. There is no love at first sight between ants of different odors.

III. The Odor and the Sense of Smell in Male Ants.

Male ants apparently bear a specific odor, beside the odor that may be incurred during their residence with nurses in the home nest. I have introduced males of different species into the nests of *Stenamma fulvum*, *Cremastogaster lineolata*, *Myrmica rubra*, *Formica sanguinea*, *Formica Schaufussi*, *Camponotus pennsyl-*

[1] "A Cause of Feud Between Ants of the Same Species Living in Different Communities," A. M. Fields, BIOLOGICAL BULLETIN, Vol. V., No. 6, November, 1903, p. 327.

vanicus, *Camponotus pictus*, *Camponotus americanus*, *Lasius latipes*, and *Lasius umbratus*, and all these males have invariably been killed within a day or two. If hybridization is to be effected among ants it will be necessary to cause the males and females to become acquainted with one another within a few hours after hatching. When hatched in the same nest, males of *Stenamma fulvum* pursue queens of *Cremastogaster lineolata* with the same ardor that they show in pursuing queens of their own species. In my mixed nests the failure of individuals of these two genera to mate was manifestly due to physical and not to psychic incompatibility.

In the summer of 1905 I had material in my stock of ants for experiments giving evidence that the male ant has at hatching the specific odor of his virgin worker-mother. My E mixed nest consisted of workers of *Camponotus pictus*, *Formica neogagates*, *Formica subsericea*, and *Stenamma fulvum*, all hatched during the last week of July, 1904, and kept in the same nest until the first day of January, 1905, when the *Stenammas* were segregated apart. They remained in segregation until August 22, 1905, when I put into their small nest, where there were ten workers and a few eggs, a fine male *Camponotus pictus*, the offspring of a virgin worker-mother who had shared the nest of these *Stenammas* until she was five months old. This young male was received by the resident *Stenammas* with evident pleasure. They licked him, regurgitated food to him, and rode on his back. He continued to live happily with them for many days. He bore a familiar specific odor, although hatched among segregated workers of his species, eight months older than any that these *Stenammas* had known; and this familiar odor made him welcome. His fate was in strong contrast to that of some of his brothers or cousins introduced into another nest. At the time of these experiments I had also a nest, marked D, of eleven *Stenamma fulvum* workers, that had hatched in a mixed nest during the last half of August, 1903, and had lived for several months with *Camponotus pennsylvanicus*, and *Formica subsericea*, but had never met a *Camponotus pictus*. These eleven *Stenammas* had lived in segregation since July 17, 1904, and were destitute of young, when on August 22, 1905, I introduced into their nest

a newly hatched *Camponotus pictus* male, the offspring of a virgin worker, a brother or cousin of the one in the E nest above mentioned. These ants of the D nest at once began to harry him, and although he was eleven millimeters long and very sturdy, while none of the *Stenammas* were more than five millimeters in length, they harried his life out within two days. Repetitions of this experiment gave similar results in every case.

The eggs from which these *Camponotus pictus* males were produced were deposited by their virgin worker-mothers in May, 1905, five months after the said mothers were separated from the *Stenammas* that the said mothers had lived with during the first five months of their lives. It therefore appears that the male progeny of virgin workers have not the progressive odor which characterized their mothers. The males have, however, a specific odor, an odor recognized by the ants through certain joints of the antennæ, and this odor is doubtless the stimulus calling forth the exceeding care given by the workers to young males with whose specific odor they are familiar.

On August 26 I put into each nest, the E and the D nests above described, two males of *Stenamma fulvum*. These males, the first of their species ever encountered by these workers, wery treated alike in the two nests. They were so eagerly grasped be several residents at once that it seemed as if they must lose their lives through the determined efforts of the workers to retain them. They were not left free for several hours; but so judicious were their virgin captors that no injury was done to the captives, and they lived in health and honor many days in these nests. In the E nest the *Camponotus pictus* male continued to be their associate.[1] In both the E and the D nests newly hatched

[1] A deälated queen *Camoponotus pictus* captured alone in the open on July 5, was kept in isolation till August 15, 1905, when she received amicably into her small artificial nest two young males of her species, the offspring of virgin worker ants. She licked them, regurgitated food to them, and during the several days that they remained under my observation, remained in close companionship with them. Later on this queen also received in amiable fashion the virgin mothers of these males, the worker-mothers having been kept by me in segregation during their whole lives. As this queen was captured near the spot in which the workers had their origin a year earlier, these ants may all have been of one colony. This queen killed young males of *Formica argentata* and *Stenamma fulvum* introduced into her nest.

Stenamma workers, from the same colony as were these males, were immediately killed.

Since the males avoid, or are indifferent to, ants of other species than their own, unless hatched among such species in artificial nests, it appears probable that they discern the specific odor of other ants. But they probably lack the sub-nose that perceives the progessive odor of workers. Male ants of various species placed under observation in one of my artificial nests, grouped themselves according to species, but did not quarrel with males of species unlike their own. I infer that the only inherent odor of males is that of their species; but that they are the medium through which the progressive odor of their female progenitors is transmitted to the egg that produces a female, the progressive odor being latent in the males and reappearing in their female descendants. Only the egg receiving a spermatozoön would produce a female, and this female would be endowed with her paternal grandmother's tendencies in progressive odor, the progressive odor thus manifesting itself only in the female line of descent. The fact that the worker progeny of a queen, sequestered from the pupa stage, will receive their queen-mother or the queen-mother's sister with equal pleasure, indicates similarity of odor in the product of the same queen's impregnated eggs.

I venture to predict that there will be found in female ants secretory glands or organs that are wanting or are rudimentary in the male, and that these organs are the producers of the propressive odor. There must be in both males and females secretory glands or organs producing the specific odor which is common to both sexes. These diverse organs might be identified through the possession of both sets by the female and of a single set in the male. It is also probable that the male lacks the glands that secrete the scent whereby the female lays down her individual path from the nest, and he may also lack the sub-nose which discerns this path-scent. The male seems to be unable to lay a path, and, in a change of domicile by the colony, he is carried bodily by the females to the new nest. It is through his appreciation of the specific odor and his lack of perception of the

progressive odor that the male is best fitted for his distinctive office in the ant world.

IV. The Progressive Odor of Queen Ants.

The change in the inherent, transmissible, progressive odor in a line of queens is probably slow and cumulative, but that such a change occurs is evidenced by the behavior of any segregated group of *Stenamma fulvum* workers, a species in which the queens generally remain in the colony in which they are produced. When workers from such a colony are segregated from the pupa-stage upward, it becomes difficult to find, in the wild nest, any queen that these segregated workers will accept as their own. In this species, I have reared worker-offspring from queens that were sequestered from all males except those of their own colony,[1] and these workers willingly associated with their worker-cousins. That the change of odor is but slight in a single generation is also shown by the fact that the worker-daughters of a queen, after having been segregated from their pupa-stage upward, and with no criterion of odor save that of their own bodies, will affiliate with their queen-mother at a first meeting, though they always examine her with exceeding care before rendering complete homage.

The gradual change in odor, through the introduction of the male element, from generation to generation, may be crudely represented by the use of letters as symbols of the odor of queens of the same species and variety.

The Roman numerals at the left denote successive generations of mated queens.

The letter *a* is used as a symbol of the odor characterizing two sister queens; the other letters as symbols of the odor inherited from the paternal grandmother.

I.	a,	I.	a,
II.	$a+b$,	II.	$a+l$,
III.	$a+b+c$,	III.	$a+l+m$,
IV.	$a+b+c+d$,	IV.	$a+l+m+n$,
V.	$a+b+c+d+e$,	V.	$a+l+m+n+o$,
	etc.		*etc.*

[1] "Notes on an Ant," *Proceedings of the Academy of Natural Sciences of Philadelphia*, December, 1902, p. 605.

The female descendants of sister queens would thus become more unlike in odor with every generation.

An odor providing the means of recognizing a maternal ancestor, or another descendant of that ancestor, may be dominant through more than one generation of females.

The fact that worker ants who have never met any queen will as joyfully associate with their queen-mother's sister as with their own mother, indicates that sister-queens have the same odor after mating that they had before mating, and that the first divergence in odor becomes apparent to the ants only in the offspring of sister-queens that mated with males capable of imparting unlike odors to their respective progeny. The worker ants, having attained the distinctive progressive odor characterizing their mothers' worker-offspring for the current year, may produce males who will each impart to his progeny the distinctive odor borne by all the female issue of the queen with whom he mates. Each generation in the line of queens would then depart farther from the odor of the queen ancestor, and we should find, as we do, colonies in which all the female inhabitants are inimical to all the female inhabitants of another colony. There would also be produced, as in colonies of *Stenamma fulvum*, where queens mate within the nest and remain to increase its population, the phenomenon of callows that, if segregated from the pupa-stage, refuse to affiliate with queens from the nest in which were deposited the eggs from which these callows issued.

During several years I have been interested in ascertaining whether adult, queenless workers would willingly accept a queen who was indisputably of another colony of their own species, and among many experiments I have never seen such an acceptance. If forced into association, escape of either party being made impossible, the workers may after a longer or shorter interval live peaceably with the alien queen, as they also may do with alien workers. But such forced alliances do not result in normal prosperity, even when a whole year is allowed for the cementing of friendship. So exacting are the ants concerning adherence to their standard of odor that they prefer a queenless state to the presence of an unknown ant-odor. Observations made by me in the summer of 1905 accord with my earlier ones. Eleven

workers of *Stenamma fulvum piceum* had been inmates of one of my mixed nests, with *Camponotus pennsylvanicus* and *Formica subsericea*, all hatched between August 14 and September 3, 1903. The *Stenammas* had been removed from the mixed nest, and kept in segregation since June 23, 1904, and had never met a queen. On August 13, 1905, I introduced into this nest a young, winged queen of the same variety as these workers, on the twenty-fourth day after I had isolated her to ensure her freedom from incurred odor. The queen fled from the group of workers and constantly tried to escape. She was attacked whenever I forced her into the group of workers, and was caught and killed by them on the ninth day of her sojourn. A deälated queen introduced later, from the wild colony to which these workers originally belonged, was also killed by them.

Since ants possess so discriminating a sense of smell, and are so exacting concerning an adherence to the criterion established for their nest, and since even those ants who have had an extended experience in ant-odors, and who have been queenless for two years, refuse to affiliate with a queen of an alien odor though of their own variety, we may hardly expect that they will voluntarily associate with queens of another species. During the summer of 1905 I introduced queens of other species into segregated, queenless groups of adult *Stenamma fulvum*, of *Formica neogagates* and of *Formica Schaufussi*, that had had their sense of smell highly educated by long association with workers of two or three different species of ants, but in every case the introduced queen was killed within a few days, in spite of her constant efforts to keep aloof from the workers.

In no species of ant have I found workers that would tolerate the presence of any queen of unfamiliar odor, nor any queen that would willingly remain among workers of unfamiliar odor. Although all species of ants have not been thus tested we may well assume that what is shown to be a fundamental trait in a few species will manifest itself in all species of the tribe.

V. Effects of the Progressive Odor in the Communal Life of Ants.

Since the queen is ordinarily the earliest occupant of the ant-nest, and since her callow young have the same odor as herself, the odor of her earliest nest must at first be the same as is that of the queen. Probably this odor is at all times dominant in the permanent nest; but as the progressive odor of the workers is gradually added thereto, the nest-aura would be thereby modified. The change in the nest-aura, cumulative with the age of the colony and the increase of the inmates, would be so gradual that all habitants of the nest would at all times find it familiar and therefore congenial. The greater dominance of the queen's odor in the earlier nest may be the cause of the persistence with which many workers cling or return to the old habitation even after the majority of the colony has for sound reason removed to a new abode.

It appears probable also that diffused ant-odor is in direct ratio to bulk of ant-body, and that a cause of the common activity of workers in adding the lesser to the larger pile of brood, sometimes even against the inhibitory effects of light, is due to the more manifest odor of the larger pile.

I have at different times during several years observed in my artificial nests a most curious phenomenon among ants that had long lived amicably together. Several or many workers were seen standing around one ant as if holding a court of inquiry concerning this associate. Sometimes the associate is proscribed, sometimes rent limb from limb. This extraordinary behavior is probably due to the victim having attained a progressive odor that is obnoxious to many other inmates of the nest because unknown to them. This might happen to an aged ant whose horde of companions were all young. It might also happen that in prowling for food, or in raids made on the nests of aliens, the worker ants would bring in alien young for food, and that this much licked and tended young would incur the progressive odor of the nurses. At a later period the introduced ant might produce a progressive odor unlike that of the multitude inhabiting the nest, and it would therefore be doomed to destruction. Ostracisms or violent

deaths, such as sometimes occur in nests where amity has long prevailed, are probably to be explained by the attainment by some of the inmates of a new and therefore an alarming progressive odor.

There may be seen among ants of the same variety, and even in the same individual, all degrees of attraction and repulsion towards other ants at a first meeting with them. Such manifestations range all the way from cuddling, caressing, cherishing devotion through indifference and inattention, distrust, suspicion, animosity and enduring, ferocious enmity. The inciting cause is doubtless the progressive odor of the visitor, and the practical end is the preservation of the chemical standard of the nest.

Whatever the action of the ants, it is always more obvious when there are numerous young in the nests, and when the nest-aura is well established.

During five years of fairly constant study of ants I have seen no evidence that their antennæ are the organs of any other sense than the chemical sense, and I am convinced that any statement concerning the behavior of ants may well be distrusted if it ignore the dominance of the olfactory sense over the conduct of the ant, the ant's almost inconceivable minuteness of discrimination in odors, or the ant's marvelous memory of odors that have been encountered. Only when ants are segregated from the pupa-stage, and full record kept of every experience of theirs in meeting other ants, can the investigator truthfully declare that ants behave in a certain manner in the presence of other ants. Moreover, as every ant acts on personal experience and individual memory, the ants should be considered singly as well as in groups and communities, when a theory of their behavior is to be enunciated. But when the total history of an ant is known, the investigator may accurately predict the behavior of that ant toward other ants. There is exceeding uniformity of behavior among ants having an identical history.

The progressive odor of the worker ants is manifestly an advantage in their communal life, since it furnishes the means whereby every ant can recognize its home and its fellow-citizens, avoiding nests and communities other than its own. The uses of this odor within the colony may also be numerous, and it may determine the distribution of labor in the ant community.

Through the male element, it probably differentiates the odor of queens of the same species, enabling the workers to find, to defend, and to cherish their own queen.

It differentiates ants otherwise alike; determines their distribution in separate communities; dictates the behavior of members of one colony toward those of another colony, and in connection with an acute sense of smell and a powerful memory, is a dominant factor in the life of the individual ant and in the structure of the ant-colony.

REACTIONS TO LIGHT AND MECHANICAL STIMULI IN THE EARTHWORM PERICHÆTA BERMUDENSIS (BEDDARD).

E. H. HARPER.

Recent work concerning the behavior of earthworms has related chiefly to their reactions to light. Since the contributions of Hofmeister and Darwin, and that of Hesse ('96) there have been a group of recent papers by Parker and Arkin, Miss Smith, Adams and Holmes, which have been devoted chiefly to the directive influence of light. In the present state of the discussion of this subject the current theory of tropisms has been called in question, according to which the earthworm is oriented directly by light. Holmes has shown that light induces a general state of activity leading to random movements of which those toward the light are checked and those away from it continued, this resulting in final orientation.

This paper aims to show that random movements are a feature of less strong light, tending to disappear with the increase of intensity, and are replaced by direct orientation in very strong light. It is also shown experimentally that the earthworm is more sensitive in the extended than in the contracted state, and that this has an important bearing upon the production of random movements. The explanation given of this is that when extended the sensitive elements of the skin are expanded over a greater surface. This is shown to have a bearing upon the production of random movements as follows: Locomotion consists of a succession of extensions and contractions and as each extension begins in a state of lower sensibility the anterior end may be projected toward the light, only to be checked when its increase of sensibility with extension makes the stimulus appreciated. Movements away from the light are not so checked. In stronger light the sensibility of the worm when contracted is sufficient to suppress movements toward the light at the outset. In such light the worm appears to be orientated without trial movements. It is important that the worms be kept in the dark before all experi-

ments, as their discrimination diminishes and random movements begin again when this is the case.

It is shown that the reactions which are typical of the life in the burrow are more definite and controlled by weaker stimuli than reactions in the open, and this may be expressed by saying that the earthworm's organization is more highly adapted for life in the burrow. Reactions in the axial direction are definite and more sensitive to stimuli than lateral movements in response to light.

The genus *Perichæta* is noted for its agility, and of its special reactions the leaping movements are the most notable.

Description of the Species.

Perichæta, the eel-worm, as it is called by gardeners, is an exotic genus of earthworms which is said to be quite commonly established in greenhouses in the old world, and also in gardens in parts of France, where they have been introduced, it is said, from the east. The only mention of *Perichæta* having been found in this country, that has come under the writer's notice, is that of Garman, who reported a species of *Perichæta* as becoming established in greenhouses in Urbana, Ill. The writer found *Perichæta bermudensis* (Beddard) in a greenhouse in Evanston, Ill. In suitable conditions of soil these worms flourish in great abundance.

The genus *Perichæta* is noted for its activity. The squirming movements which have given it its name of eel-worm are a striking exhibition of agility. This sort of movement is not confined to *Perichæta*, but is developed in the genus to an extent not found elsewhere. By alternate contractions of the longitudinal muscle bands it makes a series of leaps, by which it may waltz about for quite a distance. It reacts in this way when handled or disturbed, as when uncovered from its burrow.

The worms are of rather large size. They are found often measuring nine inches in lengh when killed fully extended. They are rather pointed at both ends. The continuous circles of setæ on each segment give the name to the family. The clitellum is a complete band or girdle encircling segments 14–16. A large pair of spermiducal glands shine through the opalescent

skin behind the clitellum, making a conspicuous mark. The dorsal pores are very prominent, exuding an abundant yellowish mucus. The everted buccal cavity is used as a proboscis, and is thrust out constantly in its feeling movements. The blood vessels are prominent, shining distinctly through the skin. The very numerous, minute, diffuse nephridia are a feature which, along with the continuous circles of setæ, have caused considerable discussion as to whether these conditions are primitive for earthworms or secondarily derived.

The Theory of Tropisms.

The orientations to light and other stimuli, which are among the most striking phenomena in the behavior of the lower animals, have received various explanations. After the first anthropomorphic explanations of these movements, based upon likes and dislikes, there came an apparent revolution of ideas bringing in explanations of seemingly great simplicity. As the physiology of plants, particularly of the higher plants, had made considerable progress towards a solid physico-chemical basis, there was a transference of conceptions based upon plant physiology to the realm of animal behavior and the orientations of the lower animals were illuminated by analogies drawn from plants. For example, we find the assertion of identity between heliotropic phenomena in plants and animals. The mechanism of the tropism was not a reflex according to this conception, but was a unique form of movement to be added to the classification of animal movements into reflex, instinctive and voluntary.

The current theory of phototropic or -tactic phenomena as applied, for example, to the earthworm, was that when light strikes one side of the animal so as to cause unequal stimulation of the two sides, it changes the tone of the muscles on the side affected. The muscles of one side are thus either relaxed or their tension is increased according as the animal happens to be positively or negatively phototropic. It is bent away from or toward the source of stimulation by the direct action of the environment upon the protoplasm. The tropism is accordingly regarded as a peculiar kind of forced movement, dependent upon the chemical nature of the protoplasm.

Jennings has shown in the case of the Protozoa and also the Rotifera that the tropism theory gives an untrue explanation of the mechanism of orientation. These animals are not directly swerved away from or toward the source of stimulation, but they have their peculiar methods of reaction and orientation in the direction of the stimuli is effected by a sort of "trial and error" method.

Reactions of Earthworms to Light.

Since Darwin's account of the habits of earthworms there has been a series of papers devoted chiefly to the directive action of light upon these forms. Parker and Arkin, Miss Smith, Adams and Holmes have studied the reactions of earthworms crawling over surfaces, exposed to light stimulation from one side.

Parker and Arkin observed the head movements of worms placed at right angles to the direction of the light and determined that 65 per cent. of the movements were indifferent, *i. e.*, straight ahead, 30 per cent. were away from the light and 4 per cent. toward it. They regarded the various head movements in different directions as due to a variety of chiefly undefined causes in addition to light and since 4 per cent. were toward the light they assume that as many of the negative responses would be due to other causes than light. So subtracting 4 per cent. from 30 per cent. the remaining 26 per cent. they regard as the measure of the negative phototactic response. Adams showed in addition that the earthworm is positive to very weak light.

The observers mentioned did not consider the question of the mechanism of orientation. Holmes takes up the current tropism theory and questions its explanation of the mechanism of orientation for these animals. He shows that the various extension movements appear to be of a simply random character, due to a general stimulation by light. The way in which orientation is effected he describes as follows. Movements that are toward the light are checked and the animal draws back and usually moves in the opposite direction. Movements away from the light do not lead to further stimulation and so are prolonged farther, and as a final result of such random movements, the worm gets into the direction of the rays, in which position the stimulation of the sensitive anterior end is least, and it then continues to move

straight ahead. Any swerving from this path leads to an increase of stimulation and hence is corrected. Holmes regards none of the movements as forced by light. All are random in direction but certain favorable ones are followed up and unfavorable ones checked by the increase of stimulation resulting from them.

Holmes proposes his theory of the "selection of random movements" only as one factor in phototaxis, not wishing to exclude the possibility of a slight amount of directive influence in the light. His reason for so doing is based on the observation of himself and the other experimenters alluded to that there is an excess of negative turnings over positive ones. Of course if the movements of the animal are random there should be an equal number of movements in the positive direction as in the negative, when one considers only the first movements occurring after stimulation. Holmes counted a number of first movements and found them about as equally divided between the positive and negative side as could perhaps be expected (23 : 27). Parker and Arkin found an excess of negative movements over positive of 26 per cent. Miss Smith (on the same basis of reckoning) found an excess of 39 per cent. and Adams, using different intensities of light, found that the excess was greater with an increase in the intensity. If the observers did not count only the first movements after stimulation but also many subsequent movements, the excess of negative movements is not against the supposition of their random character. It may be well for clearness to suppose a case. Of one hundred first movements after stimulation (when the worms are placed at right angles to the light) there should be an equal number of positive and negative, if they are purely random. But according to the theory, negative movements tend to be continued while the positive ones are checked and may be followed by negative movements. This would give rise to an excess of negative movements in any large number that were counted. Holmes says that the excess of negative movements may be due to one of three causes—accident, failure to count many of the slight positive movements which are easily overlooked, or to a slight orienting tendency of the light. Holmes undoubtedly has in mind first movements only, when he assumes that an excess of negative movements is against the supposition of their random character.

Holmes's theory of the "selection of random movements as a factor in phototaxis" is thus based upon observational evidence which is easy to verify. It is easy to observe that the movements toward the light are apt to be checked and the movements away to be more prolonged. It is less easy to note in weak light, as the final result of orientation takes longer in that case.

Absence of Random Movements in Negative Phototaxis in Very Strong Light.

All of the experimenters referred to used artificial light except Miss Smith, who used diffuse daylight. Since all of them but Holmes took for granted the direct orienting power of light, they did not care to put the matter to a crucial test. It would seem that a test of the orienting power of light would require the use of lights of various strength, and especially of very strong intensity, since the perceptive power for light is so poorly developed in the earthworm. A test of the orienting power of direct sunlight is a very easy thing to make. Place the earthworm upon a sheet of wet paper in a beam of direct sunlight from a window. The light may be passed through a water chamber. The results are sufficiently obvious as to leave no doubt of their general nature. *Perichæta* is oriented directly away from the light, when placed at right angles to the rays. The first effect is a turning of the anterior end away from the light and by a series of turns the worm gets into the oriented position and crawls directly away. Usually the result is produced without a false movement. It is immaterial whether heat effects are excluded by passing the light through water or not. A species of *Lumbricus* was experimented with and behaved in the same manner.

If the sheet of paper is turned as the worm turns, so as to keep it at right angles to the rays the worm will travel in a circle continuously. To show the difference between the orienting effect of sunlight and that of an ordinary artificial light the following experiment was tried. By using a sort of searchlight consisting of a tube of asbestos paper surrounding a 32 c.p. incandescent light and narrowed to a small aperture, the light was so manipulated by the hands as to keep it constantly directed upon the anterior end of the worm, with the worm at right angles to the

rays. In this way the worm was kept under constant stimulation and caused to turn through one complete revolution and the time required was noted. The process of turning was slow and was effected by a series of readjustments involving many trial movements in the opposite direction. Most commonly about two minutes was necessary. In twenty such cases the average time required was five minutes, the greatest time, twenty minutes.

In the beam of sunlight as before stated the worm turns continuously without trial movements. The difference in behavior in the two cases is so striking that the occurrence of an occasional positive random movement in the sunlight is plainly seen not to affect the general result. When the worm is exposed to the sunlight, if a passing cloud obscures the sun, random movements begin to appear. Miss Smith, who used diffuse daylight from a north window, observed that the worm moves in a general direction away from the light, but in an uncertain manner. Adams, using a graded series of artificial lights, showed that the per cent. of negative movements increased with the intensity. Adams did not observe the whole process of orientation since he placed the worms in an illuminated box and observed the direction of their movement after an interval of stimulation. Holmes used artificial light of only one strength. A Welsbach burner was also used to give an intermediate intensity between those before mentioned. Worms were used that had been kept in the dark and they were brought suddenly into this powerful light. They all moved away from the light with very little appearance of random movements. At each forward extension they would turn a little away from the light so that their path appeared like a curve. It is not meant to be stated that there were no random movements. But there could be no hesitation in saying that there was a decided difference in their reaction under the stronger light. Fresh worms would by a series of turns get into the oriented position frequently without a noticeable random movement. If the worms were kept in the light for some minutes, they lost sensitiveness and their random movements began to be evident.

Occurrence of Positive Phototropism.

When using a 32-candle-power incandescent light it was noticed that some individuals behaved positively. About 6 per cent. of 200 worms tested showed the positive reaction. But at a few inches distance from the light these worms would apparently become negative. Heat effects were not excluded however. The following is a typical instance. An earthworm crawling on a table moved straight toward a 32-candle-power incandescent light until within a few inches, when it began to swerve and without pausing moved in a continuous curve away from the light until it was in the line of the rays, when it continued to move in a straight line away from the light.

Difference in the Sensibility of Earthworms to Light in the Contracted and Expanded State and the Bearing of this fact upon the Production of Random Movements.

The conclusion reached is that earthworms are oriented directly by light, but owing to their low degree of sensitiveness their movements are uncertain except in very strong light. The influence of light produces a number of noticeable effects upon the behavior. First, there is a state of general stimulation or restlessness inducing locomotion. Second, in light not strong enough to produce direct orientation the worm projects its anterior end in any direction. If toward the light, the worm after stretching out its anterior end will again retract it as if stimulated. If the worm is checked only after making an extension movement toward the light, the conclusion would seem to be that the anterior end is more sensitive when extended than when in the contracted condition. One may test this conclusion by further experiment. If a light is flashed suddenly upon a contracted worm the influence of the stimulus seems to affect it gradually, leading after an interval to movements. The extended anterior end responds far more quickly to sudden changes of stimulation. The basis for this difference in reaction must be in the fact that when the head is extended the sensitive elements in the skin are spread out over more surface than in the contracted state. A simple experiment will illustrate this fact. If an earthworm is

crawling on a moist paper it may be shaded by the hand or otherwise. When the worm crawls to the edge of the shadow and thrusts out its anterior end into the light it is jerked back suddenly. But if the light be thrown upon the worm when contracted, there is no sudden response, but only a gradual awakening to stimulation, as evidenced by subsequent movements. The bearing of this observation upon the movements of the worm would seem to be as follows: The worm contracted is like an animal with its eyes partly closed. It extends its head at random, thus gradually receiving the full stimulation upon its surface. If the movement is toward the light, this causes it to contract more or less and so check stimulation. If the movement is away from the light, the oblique illumination produces less stimulation and the movement is more prolonged. An animal with eyes, as a crustacean, or an insect, is of course so organized that movements toward the light may be checked, as it were, at the outset, in the case of negatively phototactic animals.

It is to be observed that the earthworm begins these random movements while in the contracted state. After extension it draws up its body by means of the longitudinal muscles and is therefore in the contracted state. It then advances again, and at each advance there may be a random change in direction. Thus the worm begins these random movements when in the contracted state and under minimum stimulation. The nature of its locomotion and of the sensitive elements in its skin necessitates the alternation of states of low and high sensitiveness. The random movements of an earthworm under light stimulation are consequently of an entirely special character, due to causes inherent in its structure.

To recapitulate, three situations in regard to light have been described, with their characteristic reactions. First, in weak light, second in strong light and third in a situation involving change of light intensity.

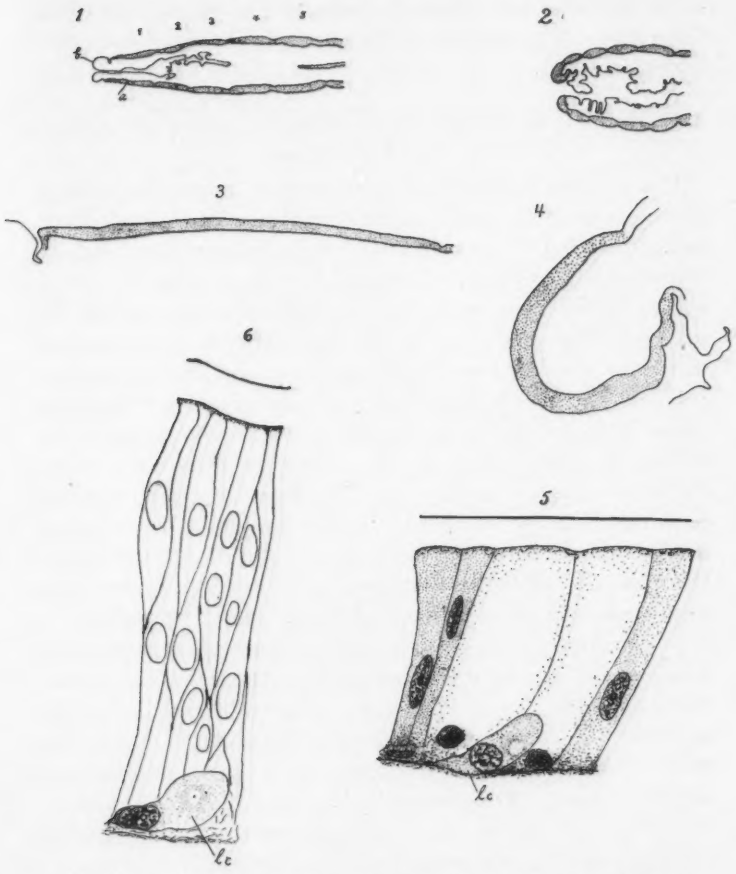
The stimulus of a change in intensity causes the animal to draw back its anterior end slightly and it then usually alters its course. When crawling under the influence of sufficiently strong light, it bends its head away from the light at each successive advance, until it gets into the oriented position. In light not

strong enough to have the directive effect its extension movements are random, an advance toward the light being checked and orientation being brought about by following up of favorable random movements. There are only two responses in reality, the checking or drawing back of the head involving the symmetrical use of the longitudinal muscles of both sides, and the turning response, involving the longitudinal muscles of only one side, that opposite to the source of stimulation. The two responses may also be combined.

The Anatomical Basis for the Difference in Sensitiveness to Light in the Extended and in the Contracted State.

The text figures introduced are intended to make clear the reason for the difference in the sensibility to light of the anterior end in the contracted and extended state. Hesse, who has worked on the organs of light perception of the lower animals, has shown the structure of the light cells in many species of earthworms and has worked out their distribution segmentally. He shows that these cells are most numerous on the first segment, and especially on the prostomium (which is fused with the first segment in *Perichæta*) and that their number diminishes rapidly on each segment as we go farther back. It is consequently the very tip of the animal (the posterior tip as well) which is most important for the perception of light, although light cells are found in small numbers over the whole length of the body.

The sections of *Perichæta* (Figs. 1 and 2) show that the first segments are subject to great extension and contraction. It was not possible to get the worm fixed in the fullest state of either extension or contraction. In Fig. 2 it is seen that the first segment is partly inrolled into the buccal cavity in the state of contraction. For further demonstration of this point the epithelial layer alone, of the first segment, is represented in the extended and the contracted state in Figs. 3 and 4. It is seen to be greatly thickened as well as inrolled when contracted. The effect of this on the light cells is seen by comparison of Figs. 5 and 6. The light cells are on the basement membrane. The thickening



The figures illustrate certain features of the worm in the extended and in the contracted state. The states of extension and contraction represented are not the most complete possible.

FIGS. 1 and 2 are sagittal sections of the first five segments of an extended and a contracted worm respectively. (*a*) body wall, (*b*) everted buccal cavity slightly protruding, which is used as a proboscis. It is to be noted that the first segment, which is the most sensitive to light, is partly inrolled in Fig. 2

FIGS. 3 and 4 are sections of the dorsal epithelium of the first segment of an extended and contracted worm respectively in the same plane as the last.

FIGS. 5 and 6 give sections of epithelium in the extended and contracted condition. (*l. c.*) light cell.

of the epithelial layer must of course tend to cut off light from these cells. The inrolling of the most sensitive region is another important factor.

The Bearing of Experimental Results upon the Habits of the Earthworm.

It is a truism that in all experiments upon animals the relation of the experimental results to the normal life of the animal should be kept in mind. The behavior of the earthworm has not been systematically studied as a whole except by Darwin. It is obvious that all the experimenters mentioned have studied the reactions of the earthworm in only one phase of its activity, and that phase is not what we should call the normal life of the worm. It is as if the experimenters had chosen the situation of the earthworm as we find it crawling on the sidewalks after a heavy rain as being its typical mode of life. None would probably admit this sooner than themselves, and doubtless they have regarded certain facts as too obvious to require mention. Does the fact that the normal life of the earthworm is carried on in a burrow affect our view of the experimental results obtained? Now the earthworm does spend a portion of its life, during the night time, crawling on the surface of the ground in search of leaves, and also during sexual activity it is less mindful of the light, as is stated. The earthworm leaves its burrow rather reluctantly. Darwin describes the earthworm as retaining the posterior end in the burrow while making searching movements in all directions in search of leaves. In drier weather we know that worms burrow deeply and seldom are found near the surface, depositing their castings in old burrows instead of on the surface.

If the worm is at home almost exclusively in the burrow we should expect those responses which are typical of the burrow life to be better organized and more definite than its activities when crawling in the open. The movements which are typical of the life in a burrow are mainly in the line of the axis of its body. Are these movements and the responses which control them of a more definite nature than its lateral movements? We may first consider the typical burrow movements in response to light. These may be imitated easily by using a screen to shade

the worm or portions of it while crawling on a moist surface, preferably covered with a thin layer of dirt.

If a worm which has been kept in the dark is placed on the moist surface, and the screen is suddenly moved so as to expose the anterior end to light, it contracts the anterior segments slightly, sometimes so slightly as to be barely noticeable, and crawls backward into the shadow. If the posterior end be illuminated in the same way the worm crawls forward into the shade, but after a noticeably longer interval. A slight twitching of the posterior end may be noticed at first, if the light is suddenly turned on. The worm always crawls forward when stimulated posteriorly, If a worm is crawling backward it can always be reversed by stimulating the posterior end. Crawling backward is of course the method by which the worm comes to the surface to eject castings. The two sorts of responses described are of the kind called " photopathic " as distinct from phototactic, and they serve of course to inhibit the worm from leaving its burrow in the light. These " photopathic " responses are very definite and the stimulus calling them forth may be quite weak light. Adams has shown that in very weak light *Allolobophora fœtida* is positive and he suggests that the worm leaves its burrow in response to the stimulus of very weak light upon its anterior end. These observations show that the movements of the worm in its burrow are very definitely controlled by the light, so far as they may come in contact with it by their more sensitive anterior and posterior ends. The middle of the worm is less sensitive to light but its sensitiveness may be shown in the following way.

If the worm is placed on the moist surface exposed to full light from overhead (a 32-candle-power incandescent was used, at a distance of 15 inches) and a screen is then brought over the posterior part of the body leaving the anterior end exposed, the worm does not draw back as when the anterior end was suddenly illuminated. Instead it begins to make random movements in various directions. It may crawl farther out into the light, thus bringing the middle portion into stimulation. This movement is however checked before the more sensitive posterior end is exposed. After a noticeable latent period showing the lower sensitiveness of the middle portion, the worm crawls back under the

shade rather quickly, but usually not completely. The commonest way in which the worm gets under the shade is as follows: It makes all sorts of random movements in every direction, and tries to burrow into the thin layer of dirt, until it accidentally gets the tip of the anterior end under the shadow of the screen. It then at once is oriented, so to speak, and crawls completely under the glass. It may crawl under as if circling around a post. The imaginary post may be exposed to the light so that the posterior part has to crawl forward into the light to get around the post. Usually, however, the anterior end travels faster so as to jerk the middle part under the screen at once.

These so-called "photopathic" reactions are consequently very definite and predictable because they are adaptations important in the normal life of the worm. As compared with the random lateral movements we see that they are controlled by weaker stimuli and are more definite. The anterior and posterior ends are more sensitive than the middle for the obvious reason that the ends alone come into contact to any great extent with light stimulation.

The lateral movements, which are typical of life outside the burrow, are as we have seen of a random nature and less definitely controlled. The worm "dashes back like a rabbit into its burrow," to use Darwin's expression, under a weak stimulus. But when crawling on the surface the same strength of stimulus produces only a general irritation and swaying random movements occur which lead to orientation away from the light only after many trials. With a higher intensity of light the worm is oriented more quickly. Thus we see that a very high stimulus is required to produce a direct sidewise movement away from the light while a very weak stimulus will cause it to move back into its burrow away from the light. The random lateral movements are aptly described by Holmes as "inconsequential vermiculations." But this description does not apply to the movements which are typical of its burrow life. The worm is as definitely adapted to the burrow and as little adapted for life in the open as some other burrowing animals of higher rank that could be mentioned. However this statement must be modified when we consider that a worm exposed to the light on the ground does not

trouble to make random movements but begins to burrow into the soil immediately. After heavy rains we see them washed out of their burrows, and crawling in unwonted places when they are unable to burrow.

Reactions to Mechanical Stimuli.

Perichæta goes through its peculiar jumping movements only under mechanical or similar stimulation, never under the influence of light, so far as we have observed. When touched with a needle on the anterior end it contracts the anterior segments slightly and may begin to crawl backward or it may go forward, lifting its head and making various random movements before settling on any direction. With a slightly stronger stimulus the anterior end turns away slightly from the stimulus. Increase the stimulus and the worm may contract the longitudinal muscles of the opposite side so as to jerk the body around 90 or even 180 degrees, and so give it a new direction. Or the worm may go off into a whole series of jerks, so that there is a complete gradation between the extent of the responses, depending upon the stimulus. More important as determining the extent of the reaction is the condition of the worm. Well-fed worms in fresh condition, when just dug out of their burrow, spring around in the liveliest fashion. If handled they give a series of movements which must make it difficult for an enemy, a bird, for instance, to pick them up before they get a chance to crawl under cover. When stimulated they exude an abundant yellowish mucus. Whether this is an offensive secretion to its enemies is not known to the writer. When a point in the middle of the worm is stimulated the body recoils away from the stimulus at that point and there is a slight swelling due to contraction of the longitudinal muscles, like the contraction and shortening of the anterior end under stimulation. Occasionally the worm may move violently toward the stimulus, but this seemed to be due to an overstimulation producing a complex of effects rather than a simple reflex.

The leaping movements of *Perichæta* are certainly the best examples of random movements that are afforded. They are exclusively adapted to those chance circumstances when the worm gets out of its burrow. They lead in no definite direction,

though they may carry the worm to a considerable distance and enable it to distract the enemy. They are a conspicuous example of the character of most movements of the earthworm, which belong to its limited life outside the burrow.

Conclusions.

The method of reaction to light of the earthworm is far removed from the sort of "trial and error method" of the Infusoria, as analyzed by Jennings. Its avoiding reaction in strong light is of the nature of a definite reflex which causes it to turn directly away from the stimulus, if the whole body is in the light, or to retreat into its burrow, if only the anterior end is stimulated, or go forward if the posterior end alone is stimulated. Methods of trial and error in reaction to light and other ordinary stimuli have clearly been supplanted by more definite responses in all but the Protozoa and certain other low types of animal life. The earthworm's reactions to stimuli, mechanical, thermal, chemical, are in general such as its nervous system and musculature would lead us to expect. The occurrence of random movements in response to all but very strong light is the outcome of the undeveloped condition of its organs of light perception, not to the want of a nervous system and musculature adapted for such simple reflexes. Diffuse organs of light perception may not respond definitely to a localized stimulus unless it is a very strong one. The trial and error method of its responses to relatively weak light are exceptional in character in comparison with its reactions to other ordinary stimuli. Its archaic type of end organs for light gives rise to a type of behavior which is to be regarded as primitive. For the trial and error method is clearly supplanted in the ascending scale of animal life, by reactions of a definite nature, in the case of the simple responses to the ordinary stimuli.

Summary of Results.

1. *Perichæta bermudensis* (Beddard) is an exotic earthworm found sometimes in greenhouses. Its active habits are one of its chief characteristics.

2. The body is less sensitive to light when contracted than

when extended, owing to the fact that when extended the sensitive elements are spread out over a greater surface and become more susceptible.

3. In locomotion, as there are alternate extensions and contractions, there is an alternation of the condition of lower and of higher sensibility. This is important particularly in the sensitive anterior end.

4. As the worm begins each extension in a condition of lower sensibility, it may project its anterior end toward the source of light. This movement is checked as soon as the increased sensibility of the extended anterior end appreciates the stimulus. Movements away from the light do not meet such a check and so are prolonged farther. Orientation is the result of a trial and error method.

5. In strong enough light, random movements toward the light are suppressed altogether, and the worm appears to move directly away from the light without noticeable trial movements. This applies to worms which have been kept in the dark and are in a perfectly fresh condition, as after a time they lose their discrimination and begin to make random movements.

6. Movements in the longitudinal direction are typical of the normal burrow life of the animal, and the axial movements initiated by the anterior and posterior ends are more definitely controlled by the stimulation of light and by a weaker stimulus than are the lateral movements. Lateral movements tend more to be random and are directed only by stronger stimuli because the organization of the worm is chiefly in adaptation to a burrowing life and not to an open air life.

7. The characteristic leaping motion of *Perichæta* is a conspicuous example of random lateral movements, adapted to life outside of the burrow. All gradations may be observed between the ordinary reaction to a slight local stimulus by jerking back, and also bending the body away, if the stimulus be stronger, up to a complete series of leaping movements.

8. Reactions to mechanical stimuli, as well as to other stimuli, chemical, thermal and electric, show that the worm is like other animals as highly organized as itself in responding to a local stimulus of an injurious nature by contracting and bending away

in a definite "avoiding reaction." In this respect the effect is like the response to very strong light. Consequently we see that the random reactions to weaker light have a special explanation and are only an apparent exception to the general form of negative response.

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SOME POINTS REGARDING THE BEHAVIOR OF METRIDIUM.

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It has recently been shown that the reactions of many sea anemones are modifiable, in dependence on a variety of internal conditions (Jennings, 1905). The purpose of the work here presented was to determine how far similar relations hold for *Metridium marginatum*. Since *Metridium* is the commonest of our sea anemones, and the one most used in investigation and instruction, it is important that its behavior should be well known. The work was suggested by Dr. H. S. Jennings, and carried out under his direction at the Marine Biological Laboratory at Woods Hole.

I. Changes in the Reactions to Certain Sorts of Food Bodies.

The point to which experimentation was first directed was the interpretation of the results of certain experiments of Nagel (1892) and Parker (1896). In Parker's experiments alternate pieces of meat and filter paper (soaked in meat juice) were given to the tentacles of one side of the disk of *Metridium*. It was found that while the meat was swallowed each time with equal readiness, the time taken in swallowing the paper increased, and after three or four trials the animal no longer ingested the paper, though the latter contained each time the same amount of meat juice as at first. After reaching this result with the right side of the disk, the same series of experiments was performed on the opposite side of the disk of the same specimen. It was found that the left side had not become modified by the experience of the right side. It at first took the paper, then by the same gradual change seen previously on the right side, it came to refuse the paper. A series of records of the times required for swallowing the meat and paper in such an experiment by Parker are given in the following table:

	Right Side.	Left Side.		Right Side.	Left Side.
1. Meat	85 sec.	45 sec.	9. Meat	70 "	35 sec.
2. Paper	80 "	90 "	10. Paper	—	85 "
3. Meat	50 "	45 "	11. Meat	40 "	30 "
4. Paper	90 "	—	12. Paper		95 "
5. Meat	40 "	45 "	13. Meat		35 "
6. Paper	105 "	55 "	14. Paper		—
7. Meat	50 "	35 "	15. Meat		35 "
8. Paper	—	105 "	16. Paper		—

What is the cause of the change of behavior in these experiments? Several possibilities suggest themselves:

1. Jennings (1905) found that in *Aiptasia* similar effects were produced, and in this case the result was evidently due mainly to changes in the state of hunger. The very hungry *Aiptasia* took meat and paper readily, but after feeding a short time it refused paper, and later it came to refuse meat also. The animal could be caused to refuse paper more readily by feeding it meat alone than by feeding paper alone or by feeding the two in alternation. It was evident that the changed reaction toward paper was due to loss of hunger. We must inquire whether this factor plays a part in *Metridium*.

2. Nagel (1892) referred the changes in reaction toward paper to a process corresponding to what we call *judgment* in higher animals; he held that the animal discovers by experience that the paper is unfit for food, and thereafter refuses to take it. Such a process in so low an animal would of course be of great interest, and the evidence for it needs to be examined carefully. Nagel held that it was owing to the lack of close nervous interrelation of parts in these animals that the experience of one side is not transmitted to the opposite side.

3. Parker sums up the phenomena shown in these experiments as follows: "The successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects, till finally the response fails entirely" (Parker, 1896, p. 116).

In my experiments I attempted to test these different possibilities, and to work out in a systematic way the various factors which modify reactions in *Metridium*.

The taking of food has been well described by Parker (1896). It is important to note that ciliary action plays a large part in the

taking of food by *Metridium*. Muscular movements of the tentacles, disk, and œsophagus also plays a part, but a less important one than in the anemones studied by Jennings (1905). The tentacles bearing bits of food are bent toward the mouth, and the cilia of the tentacular surface carry the food toward the mouth opening. The cilia of the œsophagus are usually beating outward, but when food enters the mouth the stroke of the cilia of the part in contact with the food becomes reversed, so that the food body is conveyed inward (see Parker, 1896, 1905). I have found that the reversal of the œsophageal cilia is frequently caused in *Metridium* by indifferent solids, such as filter paper, so that such bodies are ingested.[1] There is much variation in regard to this matter, some individuals take filter paper readily, others slowly and only at times, others not at all. As we shall see later, this depends largely on the degree of hunger.

We will now take up experimentally the various possibilities of modification above distinguished. In studying these matters, it is most important that specimens which are fresh and in good condition should be used, otherwise clear results will not be obtained.

1. *Hunger.*—Conditions of hunger and satiety affect the food reactions of *Metridium* in a most decided way. When the animal is very hungry (and in good condition otherwise), the column is extended, becoming long and slender, while the disk is widely spread, and the tentacles extend a considerable distance beyond its edge. If the animal remains contracted, it can often be induced to extend by placing a piece of clam meat or some meat juice on the infolded disk. Two or three applications of food will often cause the most obstinately contracted specimens to expand beautifully. If now a piece of mussel of considerable size (having an area equal to the cross section of the column, with a thickness of three or four millimeters) is brought near the edge of the disk, so as to come in contact with the tips of two or three tentacles, a decided reaction is produced. The tentacle tips adhere to the meat, and the tentacles and adjacent parts of the disk contract quickly, so that the piece of meat is drawn inward. It

[1] This was possibly due, as Parker (1905, 1905*a*) has set forth, to the paper's having been touched by the fingers; this matter was not tested.

thus comes in contact with many other tentacles, these bend down upon it. Then all bend over toward the mouth, while at the same time this portion of the disk contracts. Thus the food is brought nearer the center of the disk. The mouth meanwhile opens, and the food is passed into it, partly by the ciliary action of the tentacles, partly by muscular contractions of tentacles, disk and mouth. The latter factors play a more important part in the reaction of a hungry specimen to a large piece of food than does ciliary action.

After ten or a dozen good-sized pieces of meat have been swallowed, the reaction becomes much slower. If the meat is brought in contact only with the outer tentacles, these no longer react, and such food is not taken. If placed on the inner tentacles, the meat is slowly transferred to the mouth, where it is swallowed. The animal is frequently in this condition when brought into the laboratory; food placed on the outer tentacles is refused, while that on the inner tentacles is taken.

The reaction of the tentacles becomes slower as more food is taken, so that the process of ingestion takes a much longer time than at first. Finally, all the tentacles cease reacting to food, and it is not carried to the mouth. But if the meat is placed by the experimenter directly on the mouth, it is ingested. This appears to take place almost alone through the action of the cilia; the reversal of the cilia seems to be more nearly independent of the physiological states of the animal than are the contractions of the muscles. The mouth never reaches a condition where it rejects pieces of mussel placed directly upon it. So much food may be taken that the body becomes puffed out to form a swollen sack, yet new pieces are forced inward. Large pieces of meat may however be refused even when placed directly on the mouth, the lack of assistance from muscular contractions appearing to make it impossible for the cilia to draw them inward. The feeding may be carried so far as to cause internal disturbance, resulting in the disgorgement of the food. But immediately after such disgorgement the mouth will take new food. Sometimes when the animal is nearly filled, a large piece of meat placed on the mouth is partly swallowed, then partly disgorged by a convulsive movement, then the swallowing is resumed. This may happen repeatedly.

The loss of reaction on the part of the tentacles after much food has been taken is not due to fatigue resulting from their activity in taking food. This is demonstrated by the following facts: (1) The animal may be fed from one side of the disk till it is satiated. Now meat given to the opposite side of the disk is not taken, though the tentacles of this side have not been active, and so cannot have become fatigued. (2) Seven hours after the animal has been fed all it will take, the tentacles still refuse to take food, though they have had this period for recuperation. Actual fatigue, as we shall see later, lasts but a few minutes.

The effects of hunger and satiety are further seen in the reactions of *Metridium* to indifferent bodies, such as bits of filter paper. These are commonly taken readily by hungry specimens of *Metridium*. The tentacles react to them, just as to meat, so that they are carried to the mouth. Here they cause the reversal of the ciliary movement in the same way as does meat, so that they are carried inward. But after the animal has been fed a considerable quantity of meat, it will no longer take filter paper. First the outer tentacles refuse it, later the inner tentacles, and finally the mouth. A piece of filter paper placed squarely on the mouth no longer causes the reversal of the stroke of the cilia of the œsophagus, so that it is not carried inward.

The fact that the reversal of the cilia under such stimuli depends on the physiological state of the animal is one of much interest. It shows that the cilia are not entirely independent of such states, as some other facts would seem to indicate.

Seven hours after the animals had been fed an abundant meal of mussel meat, they still refused to take filter paper, though before the meal paper was taken readily.

Thus it is clear that the state of the processes of metabolism is in *Metridium*, as in other sea anemones, a most important factor in determining behavior under mechanical and chemical stimuli. But it is equally clear that this will not explain the results of Parker's experiments, described in the first paragraphs of this paper. Parker found that after one side of the disk has refused to take paper, the other side still accepts it. In repeating

Parker's experiments, I fed in one case six successive regions of the disk, each till it had rejected food; the next would then take it as readily as at first. This refusal then cannot be due to a general lack of hunger, and we must examine the other explanations that have been given.

2. "*Judgment.*" — If the animal comes to reject paper through experience of the fact that the paper is not good for food, there must be some way in which this experience is obtained. It might be supposed that this comes through swallowing the food; being indigestible, its effect after swallowing might cause the animal thereafter to reject it. This was tested by preventing the swallowing of the paper. The animal was fed meat and paper in alternation, as in Parker's experiments. But after the paper had been carried to the mouth and was passing down in the œsophagus, it was removed with a fine pair of tweezers. This is easily done without disturbing the animal. Thus the bits of paper never reach the digestive cavity. Yet the animal comes to reject them as quickly as before. After a few alternations of meat and paper, only the meat being completely swallowed, the animal ceased to take the paper, while it still accepted the meat. Hence the effect of the paper after it reaches the digestive cavity is not the cause of its rejection.

Furthermore, nothing like a contrast or comparison between the meat and the filter paper is necessary in order to induce the rejection of the paper. If successive pieces of paper were fed alone to the anemones, they soon came to reject these as before. In such cases it is noticeable that the animal takes a larger number of pieces of paper than when the paper is fed in alternation with meat. The number of pieces required is about the same as the number of pieces of meat and paper together that result in rejection of the paper when the two are given in alternation. This fact throws some light on the cause of the rejection, as we shall see later.

3. *Repetition of Weak Stimuli, till Effect Fails.* — Is the loss of the positive reaction to the paper due to the general fact that weak stimuli, when repeated, gradually lose their effect? This was tested by excluding this factor from the experiments, in the following way. A given specimen was first tested and found to

accept filter paper (in some cases plain, in others soaked in meat juice). After this first test, the same region of the disk was fed successive pieces of meat, which were all readily taken. After eight to twelve pieces of meat had been accepted, a piece of filter paper like that originally accepted was given to the same region of the disk. *It was not accepted.* This experiment was repeated with many specimens, always with the same result. This result was likewise reached if the animal was not allowed to complete the swallowing of the meat, the latter being removed after it had passed into the œsophagus. This, of course, shows conclusively that loss of hunger is not the cause of the change of reaction toward the paper.

The placing of meat juice on a certain region of the disk causes the food reaction, as Parker has shown. If this experiment is tried successively a dozen times in the same region of the disk, the animal comes to reject filter paper in this region, as in the experiments described in the foregoing paragraph.

Thus it is not necessary that weak stimuli should be repeated in order that the animal shall reach a state in which it fails to react to them. Repetition of strong stimuli (meat) causes failure to react to weak stimuli just as readily as does repetition of the latter. Repetition of strong stimuli alone, of weak stimuli alone, and of the two in alternation, all have the same effect ; the animal ceases to react to weak stimuli.

In all cases in which meat is fed to a given region, moreover, the reaction to strong stimuli ceases some time later than that to weak stimuli. After giving a certain region sixteen to twenty pieces of meat, meat is no longer accepted here, though other regions of the disk take it readily.

4. *Fatigue.* — The facts brought out in the foregoing paragraphs seem to make possible a clear interpretation of the rejection of the paper. It is evidently a case of plain fatigue. After stimulating a certain region of the disk a number of times, it ceases to react — first to weak stimuli, then to strong stimuli — though other parts react as before. The same results are produced whether the successive stimuli are all strong or all weak, or partly strong and partly weak. It appears evident therefore that it is the reaction of the animal, not the precise character of

the stimulus, that causes the fatigue. This is perhaps what should be expected when the nature of the food reactions is taken into consideration. In taking food the region in contact with the food produces a very large quantity of mucus, enveloping the food body. It is not surprising that successive immediate repetitions of this excessive production of mucus gradually exhausts the region. As is usual in fatigue, strong stimuli may produce reaction for some time after weak ones have failed.

The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is frequently as ready to take food as before — provided the animal is still hungry.

Nagel and Parker have held that the result of their experiments " illustrates the extreme looseness, or even independence, of the nervous activities of the two sides of the animal " (Parker, 1896, p. 116) — since the effects of the experience of one side are not transmitted to the other side. With the recognition that these results are a simple matter of fatigue, they perhaps cease to have any bearing on the question of the closeness or looseness of nervous interconnection. In the highest organisms, as man, fatigue induced by repeated contractions of a finger of the left hand, in erogographic experiments, is not transmitted appreciably to the right hand. But the experience gained by touching a hot iron with the left hand would nevertheless later prevent the right hand from touching it.

II. Other Modifications in Behavior.

A very peculiar modification of behavior is seen in the following: A specimen refuses to take filter paper, though it still takes meat. After it has thus refused paper, two or three pieces of meat are given in succession, and taken readily. Now the bit of paper is again placed on the disk, and it too is swallowed. Clearly, the uninterrupted taking of a number of pieces of meat changes the physiological condition of the animal in some way, preparing it for the taking of any object with which it comes in contact. (After a larger number of pieces of meat, the paper is refused, as we have before seen.)

Acclimatization to weak stimuli is readily demonstrated in fresh, active specimens of *Metridium*. If a light stream of water

is directed with a pipette against the expanded disk, the animal contracts strongly. Waiting till it has again expanded, the stream of water is directed upon it as before. This time it does not react. In specimens that are not in good condition, this change of behavior cannot be seen. The animal does not contract at all save under strong stimuli, and if such are repeated, it contracts as at first.

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THE INFLUENCE OF THE NERVE ON THE REGENERATION OF THE LEG OF DIEMYCTYLUS.

CECIL SHEPARD HINES.

The following experiments were carried on at the suggestion of Professor Morgan, for the purpose of ascertaining whether regeneration in the leg of *Diemyctylus* is dependent on its connection with the nervous system, as has been found in the case of other urodeles, or whether the supposed result may not have been due to unintentional injury to the blood supply. The hind limb was chosen for operating on account of its larger size. The general course of procedure was to cut the nerve in the upper part of the leg *without injury to the artery*, and then amputate the leg at the knee joint. After a period of a little more than three weeks the new part can be clearly recognized as a dark protuberance sharply contrasting with the lighter color of the surrounding skin.

In the first lots the nerve was cut as near the proximal end of the femur as possible. A longitudinal slit through the skin was made with a sharp knife. The muscles were then separated until the nerve was brought into view. Care was taken not to injure the blood vessel which closely adheres to the nerve and is almost inseparable from it. If the operation were performed without injury to the blood vessel and the leg showed a resulting paralysis it was amputated at the knee. For comparison an equal number of salamanders had the leg cut off without injuring the nerve or blood vessel. The results obtained from the first series seemed to show that regeneration in *Diemyctylus* was in no way dependent upon the nerve. The proliferation of new material began as soon in those in which the nerve had been cut as it did in the checks. Nor did the amount of material regenerated seem to be affected in any way. There were, it is true, great variations in the rate of regeneration, but these seemed to arise from purely individual differences, and to bear no definite relation to the presence or absence of the nerve connection. In two checks operated upon on the same day and kept in the same

aquarium, so that external conditions could play little, if any, part in the result, an interval of ten days or more might occur between the earliest and latest appearance of proliferation. The results obtained after cutting the nerve at this level may have been due to the presence of collateral nerve-connection sufficient to give the required stimulus to the tissue ; for as was later clearly shown, the nerve is an important factor in the regeneration.

In the succeeding series the nerve was cut through the pelvic girdle close to the backbone, in the hope of more completely cutting off the nerve supply of the limb. The incision necessarily went through into the body cavity as the nerves given off from the spinal cord lie close to the inner wall and are covered only by cœlomic epithelium. The operation is by no means as serious as would be imagined, since the wound heals completely in three days. During this time the animal acts in a perfectly normal manner except for the injured leg. Instead of using separate individuals for checks as before, both legs of the same individual were amputated, but the nerve was cut on one side only. The males are much more difficult to operate upon than the females, on account of their greater muscular development, whereas in the female the pelvic girdle stands out prominently and the body wall is thin. In the males the girdle is not visible externally and is overlaid by a thick musculature which renders operating upon the animal at this point difficult.

On November 26 a set of seven salamanders was operated upon as described above. They were not again observed until the forty-fifth day. At that time both legs of each individual had proliferated material to a greater or less extent. The side used as a check could be identified in every case but one, by its far greater amount of proliferated material.

In the exception the animal assumed a peculiar green color, evidently from a disease, and at a later period both legs were entirely sloughed off. This set was continued under observation until the eighty-third day, at which time there was still a decided difference between the appearance of the two sides, although by no means as pronounced as before. The check showed in each individual the foot plainly differentiated, while in only two instances was this the case upon the other side, and even in those cases to a much less extent.

Later I operated upon at least thirty salamanders in several lots. Some of these were starved while others were well fed. The abundance or lack of food did not seem to be a factor in the rate of regeneration. Salamanders which were reduced almost to "skin and bones" showed the same comparative amount of regeneration as well-fed individuals. The influence of food did show itself, however, in the amount of material proliferated. During starvation an individual shrinks greatly in size and proliferates much less material for the same relative amount of regeneration as a well-fed companion.

To ascertain whether the blood supply was a factor in regeneration the artery of several individuals was cut just above its entrance into the leg, the nerve being left intact. The result showed that the leg regenerated at the normal rate. However, not much stress can be laid upon this experiment, owing to the rapidity with which a sectioned blood-vessel heals.

That the circulation in the leg may have continued to some extent after the operation in those individuals whose nerve as well as artery had been sectioned near the backbone was shown conclusively by the following experiment. A salamander was taken and a cut made in the pelvic region as before. Then a vein was severed in the lower part of the leg. This continued to bleed freely for a considerable time, as would not have occurred had the total blood supply been cut off. The collateral blood supply probably still brought blood to the limb. Similarly the collateral nerve supply may in the first series of experiments have sufficed to keep the regeneration up to the same rate as in a limb in which the nerve was not cut.

In a number of cases regeneration did not set in at all on the side on which the nerve had been cut. At least, after a period of two months and a half there was not the least sign of proliferation, while in the normal course of regeneration the new part appears in about twenty-five days. This lack of regeneration is probably due to the distal end of the nerve being displaced, and in consequence the regenerating nerve was unable to grow down its old path along the degenerated nerve, but was turned aside. Consequently not even a retarded regeneration occurred.

The most important work bearing on the question of the rela-

tion between the nerve and the regeneration of the leg is that of Wolff.[1] He found that if the nerve-cord were destroyed in the region of origin of the leg nerve that the leg regenerated at the normal rate. Since the spinal ganglion was left after this operation, its presence may have sufficed to produce the result. In fact, nerves were found in the new foot. In order to remove the ganglion also, a piece of the spinal column was cut out including cord and ganglion. Six individuals that survived this operation showed that after the first proliferation of new material had taken place growth came to a standstill for a time and then began again. The result suggests, Wolff thinks, that the standstill was due to the lack of nerve connection, while the renewal of growth was due to the reëstablishing of a new nerve connection. In fact the disabled leg showed some signs of having regained its power of motion.

Wolff discusses the question whether the period of standstill may not have been due to the lack of function or activity of the leg while its later growth was due to its regaining its locomotor function. He argues that this is probably not the case, but that the nerve connection is directly responsible for the result.

A student of Busfurth's, R. Rubin,[2] has obtained similar results. What part the nervous connection plays in these cases is still obscure. Morgan and Davis[3] have found that for the regeneration of the tail of the tadpole, the presence of the notochord and not the nervous system is the important factor.

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[1] *Virchow's Archiv*, CLXIX., 1902.
[2] *Archiv Entw. Mech.*, XVI., 1903.
[3] *Archiv Entw. Mech.*, XV., 1903.

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AN EXAMINATION OF THE METHODS FOR THE MICROCHEMICAL DETECTION OF PHOSPHORUS COMPOUNDS OTHER THAN PHOSPHATES IN THE TISSUES OF ANIMALS AND PLANTS.

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(From the Hull Anatomical Laboratory, University of Chicago.)

The microchemical reaction for the detection of phosphorus in the tissues of animals and plants introduced in 1898 by Macallum ('98) is a modification of that devised in 1893 by Lilienfeld and Monti ('93). These investigators attempted to demonstrate the distribution of phosphorus in tissues by subjecting the latter for some time to the action of a solution of ammonium molybdate in nitric acid, after which they were treated with a solution of pyrogallic acid. The nitric molybdate reagent was supposed to liberate the phosphorus from its organic combinations, to convert it into orthophosphoric acid, and finally to precipitate the latter as the yellow phosphomolybdate of ammonium. The further treatment of the tissues with pyrogallic acid had for its object the reduction of the ammonium phosphomolybdate to a lower oxide of molybdenum, which, according to Lilienfeld and Monti had a brown or black color. In this way the pale yellow precipitate containing the phosphorus was converted into a dark-colored precipitate which could be easily studied under the microscope.

The importance of a microchemical reaction which would enable us to determine accurately the distribution of the compounds of phosphorus not only in the tissues but also in the parts of the cells of the tissues can hardly be overestimated. It is therefore